

## TASK-DEPENDENT CHANGES IN CUTANEOUS REFLEXES RECORDED FROM VARIOUS MUSCLES CONTROLLING FINGER MOVEMENT IN MAN

By A. L. EVANS, LINDA M. HARRISON AND J. A. STEPHENS

*From the Department of Physiology, Rockefeller Building, University College and  
Middlesex School of Medicine, Gower Street, London WC1E 6BT*

*(Received 28 February 1989)*

### SUMMARY

1. Cutaneous reflex responses have been recorded from muscles involved in the control of finger movement following electrical stimulation of the digital nerves of the fingers in man.

2. Recordings have been made while subjects performed various manual tasks.

3. Reflexes recorded while subjects performed a relatively isolated finger movement consisted of an initial short-latency increase in muscle electrical activity, followed by a decrease, followed by a prominent longer-latency increase. The long-latency excitatory component was smaller or absent during those grips used in the present study.

4. The short-latency excitatory (E1) and inhibitory (I1) components of the cutaneomuscular reflex response are mediated via spinal pathways. The second longer-latency excitatory component (E2) is of supraspinal origin, requiring the integrity of the dorsal columns, sensorimotor cortex and corticospinal tract (Jenner & Stephens, 1982). The results of the present study suggest that one or more of these supraspinal pathways is more active when a finger is used in a relatively isolated manner than when the same finger participates in any of the gripping manoeuvres used in the present experiments.

### INTRODUCTION

It is well known that cutaneous reflex responses may be dependent upon the behavioural context in which they are elicited. During cat locomotion, for example, a weak cutaneous stimulus applied to the dorsum of the paw produces reflex excitation of flexor muscles during the swing phase of the step cycle, but if the same stimulus is applied when the limb is in the stance phase, enhanced extensor activity results (Forssberg, Grillner & Rossignol, 1975, 1977; Prochazka, Sontag & Wand, 1978). In man, Kanda & Sato (1983) have described modulation of reflex activity elicited by non-noxious stimuli during the different phases of the step cycle.

In the present study we have recorded cutaneomuscular reflex (CMR) responses from various muscles controlling finger movements in man as they participate in different manual tasks. It will be shown that the cutaneous reflex responses of the

hand muscles, like those in the lower limb muscles involved in locomotion, are dependent upon the behavioural context in which they are elicited.

Preliminary accounts of these experiments have been presented to the Physiological Society (Evans, Harrison & Stephens, 1986, 1987).

## METHODS

Recordings have been made from the right upper limbs of seventeen apparently healthy right-handed volunteers (ten male, seven female) aged 18–40 years. Ethical permission was obtained from the Middlesex Hospital Ethical Committee.

### *Experimental procedure*

Two series of experiments were carried out. In the first, reflexes were recorded from the first dorsal interosseous (FDI) muscle while subjects performed a series of eight different tasks. The order in which the following manoeuvres were carried out was varied randomly. Each manoeuvre was sustained throughout the period of stimulation.

(1) With the hand flat on a table top, an isometric abduction of the index finger was performed against resistance (abduct).

(2) With the hand flat on a table top, all the fingers and thumb were spread out (spread).

(3) The weight of the arm was supported on the index finger alone. The remaining fingers were flexed (index support).

(4) All the fingers and thumb were spread and the weight of the arm supported (hand support).

(5) A pen was held with the index finger and thumb opposed and the pen supported by the lateral border of the terminal phalanx of the middle finger (tripod grip; Wynn-Parry, 1966).

(6) A 124 mm diameter plastic ball was gripped with all fingers and thumb exerting approximately equal pressure (ball grip).

(7) A cylindrical object, such as the handle of a squash racquet, was held (power grip; Napier, 1956).

(8) Writing was performed (dynamic tripod grip; Rosenbloom & Horton, 1971).

In a second series of experiments using five of the same subjects, further recordings were made from the first dorsal interosseous and three other muscles involved in the control of finger movement: abductor digiti minimi (ADM), middle finger extensor digitorum communis (MFEDC) and ring finger flexor digitorum sublimis (RFFDS). In these experiments each subject performed two manoeuvres repeated three times. The first involved using the relevant finger in such a manner that a relatively independent muscle contraction was produced. For FDI, this was abduction of the index finger; for ADM abduction of the little finger; for MFEDC extension of the middle finger; and for RFFDS flexion of the ring finger. The second requirement was to perform a power grip when each muscle being studied participated with other synergistic muscles.

### *EMG recording and electrical stimulation*

In the first series of experiments muscle electrical activity was recorded from the right first dorsal interosseous muscle using Beckman type 650466 silver–silver chloride surface electrodes (diameter 11 mm, central contact 2 mm), 20 mm centre to centre, attached to the skin by double-sided adhesive rings over the belly of the muscle and making contact by conductive jelly.

In the second series of experiments modified neonatal ECG electrodes were used (ARBO Pink H82V, Henley's Medical) to make a pair of bipolar surface electrodes consisting of two silver discs (diameter 10 mm), 20 mm centre to centre, making contact with the skin through conductive adhesive gum. Recordings were made from FDI, ADM, MFEDC and RFFDS. Electrodes were attached to the skin surface over the mid-belly of the muscle under study.

The EMG signals were amplified and filtered ( $-3$  dB at 20 Hz and 10 kHz) using a Medelec MS7 EMG machine.

Single electrical stimuli at a strength twice threshold for perception, pulse width 100  $\mu$ s, were delivered at 3 s<sup>-1</sup> (constant interstimulus interval) using a constant-current stimulator (Medelec

IS/C) via ring electrodes (Medelec E/DS-K 53052). These were attached on either side of the proximal interphalangeal joint of the index finger for FDI, the little finger for ADM, middle finger for MFEDC and ring finger for RFFDS. This intensity of stimulation is not unpleasant and produces a sufficiently large response to be clearly identifiable after a short period of averaging.

#### *Reflex recording*

Subjects were asked to perform each manoeuvre in such a way that the EMG signal remained constant at a level 10–20% of maximum EMG obtainable while performing a relatively independent contraction for that muscle, as described above. This level of EMG could normally be maintained for several minutes before any sign of fatigue. Subjects were aided in this by a voltmeter displaying the EMG level. When a steady contraction was achieved, stimulation commenced. During writing the EMG level was not controlled. The EMG signals were full wave rectified and averaged for 512 or 1024 sweeps time-locked to each stimulus. In the first series of experiments a Medelec (MS7) averager was used. In the second series the amplified and filtered EMG signals were digitized, rectified and averaged using a Cambridge Electronic Design 1401 computer interface with a Sperry 50 microcomputer.

#### *Needle EMG recording*

Needle EMG recordings were made using Medelec type E/NO1 monopolar concentric electrodes (exposed core area 0.019 mm<sup>2</sup>).

#### *Median nerve sensory volleys*

It is important in these experiments to establish that the afferent input volley set up by the electrical stimulation is not affected in some way by the changing position of the hand and fingers in the different tasks. Thus, in two of the subjects, sensory nerve volleys were recorded from the median nerve at the wrist using Beckman surface electrodes while the subject rested the arm on the table, then during abduction of the index finger and finally during a ball grip. The signal was amplified and filtered (–3 dB at 20 Hz and 10 kHz) and averaged for 128 sweeps time-locked to each stimulus applied to the index finger as above. In these experiments the mean peak-to-peak amplitude of the afferent volley recorded during these three situations was 9.6, 9.3 and 10.1  $\mu$ V respectively for one subject and 17, 15.9 and 17.7  $\mu$ V respectively for the other. It was therefore concluded that the sensory volley elicited by digital nerve stimulation did not change significantly with task.

## RESULTS

Electrical stimulation of the digital nerves of the index finger produces a marked reflex modulation of on-going muscle activity recorded from FDI (Caccia, McComas, Upton & Blogg, 1973; Jenner & Stephens, 1982). An example is shown in Fig. 1. Typically, for abduction of the index finger, the reflex has three easily identifiable components in the first 100 ms. These comprise a short-latency increase in EMG (E1), then a decrease (I1), followed by a further increase (E2).

In the present study (seventeen subjects, seventeen recordings) the mean latency of the first component (E1) was 34.8 ms (s.d. 5.2 ms), the following reduction (I1) 48.8 ms (s.d. 4.8 ms) and the second increase (E2) 57.8 ms (s.d. 5.4 ms).

The latency of each reflex component has been measured as it intersects the mean background EMG level. The peak amplitude of each component was measured for all recordings and normalized with respect to background. For the second series of experiments the area under each peak was also measured and normalized with respect to background.

*Task-dependent changes in the cutaneomuscular reflexes of first dorsal interosseous muscle*

Figure 2 shows the results of an experiment in which CMR responses of FDI were recorded while a subject performed eight different tasks. It can be seen that the

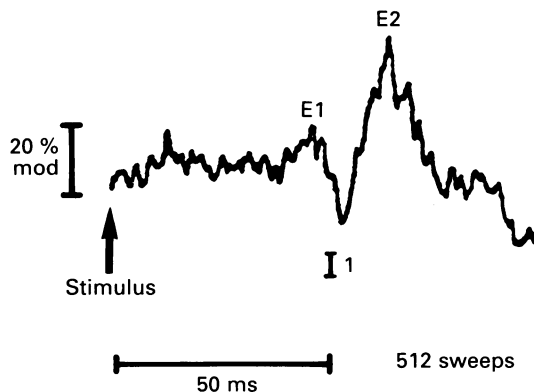


Fig. 1. Cutaneomuscular reflex response recorded from first dorsal interosseous muscle during sustained voluntary abduction of the index finger in a normal adult subject following electrical stimulation of the digital nerves of the index finger. During the recording, the subject was required to maintain a force of contraction such that the electrical activity recorded from the skin over the surface of first dorsal interosseous muscle remained at 10–20% of that associated with a maximum voluntary effort. At the same time single electric shocks at a strength twice threshold for perception were delivered to the digital nerves of the index finger at  $3 \text{ s}^{-1}$ . The record shows the averaged rectified EMG signal time-locked to each stimulus. The first component of the reflex response consists of an increase in muscle electrical activity (E1), in this example at 40 ms. This is followed by a decrease (I1) at 50 ms. There is then a second large increase in EMG (E2) at 57 ms. The Figure shows the typical appearance of a reflex with a dominant E2 component recorded during index finger abduction. Vertical calibration bar: 20% modulation (mod) of mean EMG level; 512 sweeps.

relative amplitudes of the different components of the CMR responses changed according to the task in which FDI participated. For the manoeuvres shown on the left of the figure, the long-latency E2 component of the response was larger than the earlier E1 component. In contrast, the E2 component was absent in this subject for those manoeuvres shown on the right. Table 1 shows that similar changes in reflex configuration were observed in all seventeen subjects. For the majority of subjects an E2 component was present during manoeuvres (5)–(8) but it was usually smaller than for manoeuvres (1)–(4). In detail, during the power grip the E2 component was absent in eight out of sixteen subjects and reduced in amplitude in the remainder. During ball grip, the E2 component was absent in five out of seventeen subjects and reduced in ten subjects. During tripod grip the E2 component was absent in three subjects, reduced in six and increased in two. Finally, during writing the E2 component was absent in five subjects, reduced in six, unchanged in one and increased in one.

During tasks (1)–(4) the E2 component of the reflex response in FDI was dominant

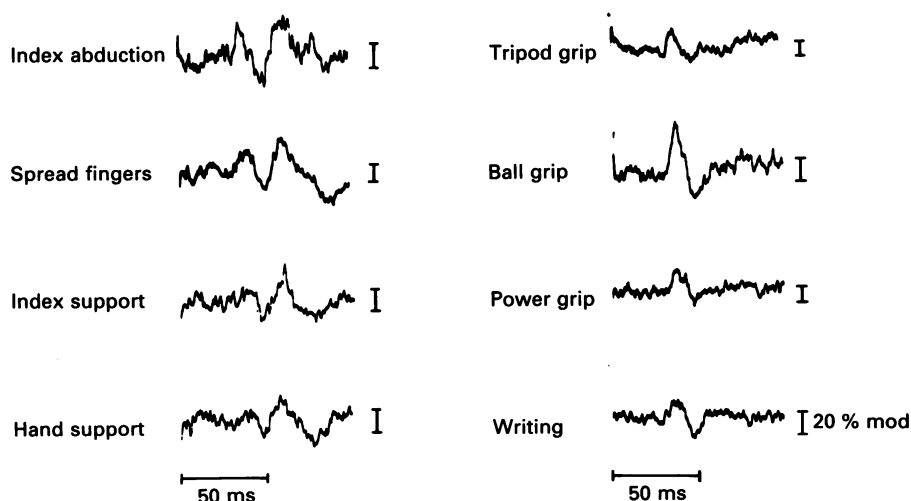


Fig. 2. Cutaneomuscular reflex responses recorded from first dorsal interosseous muscle while the subject performed eight different manoeuvres. In each case a steady contraction was made such that the same level of EMG activity was maintained (10–20% of that associated with a maximum voluntary index finger abduction). Same recording technique as Fig. 1. The left-hand column shows recordings made during four relatively isolated finger manoeuvres. In each case the long-latency E2 component of the response is dominant. The right-hand column shows recordings made during four types of grip. In these particular recordings the long-latency E2 component is absent. Vertical calibration bar: 20% modulation (mod) of mean EMG level; 512 sweeps in each recording.

TABLE 1. Mean peak amplitudes for the three components of the CMR response recorded from the first dorsal interosseous muscle during eight different manoeuvres. The number of subjects is shown by *n*. Mean peak amplitudes are expressed as a percentage of the mean EMG level (s.d.). For each component, manoeuvres (2)–(8) have been compared with abduction, using the *t* test for paired data, \**P* < 0.001, †*P* < 0.01, ‡*P* < 0.05

Manoeuvre	<i>n</i>	E1 peak amplitude	I1 peak amplitude	E2 peak amplitude	E2/E1 ratio
(1) Abduct	17	17.1 (5.8)	19.1 (11.9)	32.2 (16.0)	1.9
(2) Spread	16	18.1 (5.2)	16.3 (6.4)	32.2 (12.3)	1.8
(3) Index support	16	18.5 (7.6)	18.0 (10.9)	29.2 (15.4)	1.6
(4) Hand support	17	19.9 (7.7)	14.1 (7.5)†	26.0 (13.1)	1.3
(5) Tripod grip	15	19.7 (9.7)	12.0 (7.8)‡	13.0 (9.3)*	0.7
(6) Ball grip	17	25.9 (9.3)*	17.1 (8.5)	13.3 (11.8)*	0.5
(7) Power grip	16	21.0 (6.2)	8.0 (7.3)†	10.6 (13.7)*	0.5
(8) Writing	13	16.8 (6.4)	12.3 (8.3)	7.4 (7.3)*	0.4

in the majority of subjects (fifty-two out of sixty-six recordings, 79%). During tasks (5)–(8) the E1 component was dominant (forty-six out of sixty-one recordings, 75%).

Statistical comparison of these results is shown in Table 1 where the peak amplitudes for each of the movements (2)–(8) have been compared with abduction

(manoeuvre (1)) within individual subjects using the *t* test for paired data for each of the three components of the CMR response.

The amplitude of the E1 reflex component in FDI remained relatively constant for all the tasks. It did not differ significantly from the values of E1 recorded during abduction except for the ball grip where the majority of subjects (fourteen out of seventeen) showed an increase in E1 amplitude as is shown for the subject in Fig. 2.

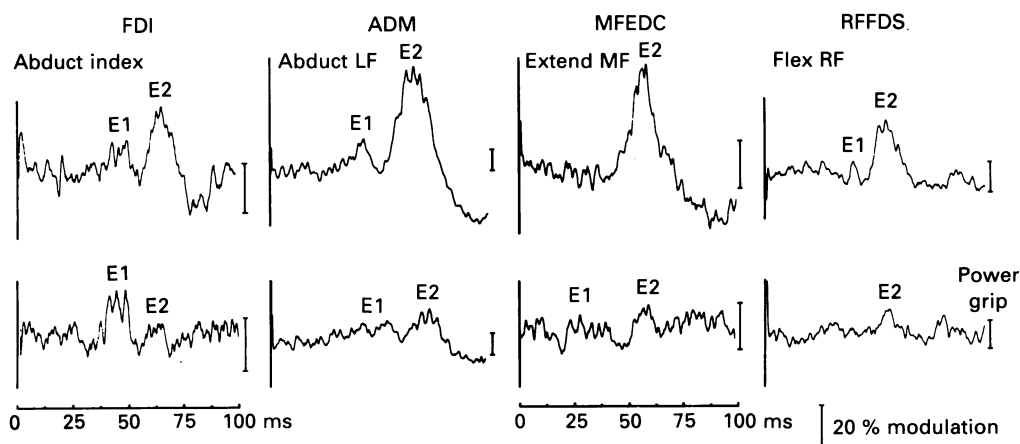


Fig. 3. Cutaneomuscular reflex responses recorded from first dorsal interosseous (FDI), abductor digiti minimi (ADM), the middle finger extensor digitorum communis (MFEDC), and the ring finger flexor digitorum sublimis (RFFDS) while the subject either used the relevant finger in a relatively isolated manner (top row) or during a power grip (bottom row). The relatively isolated contractions were abduction of the index finger, abduction of the little finger, extension of the middle finger, and flexion of the ring finger. In each case the subject was required to maintain a force of contraction such that the electrical activity recorded from each muscle remained the same at 10–20% of that associated with a maximum voluntary effort. At the same time single electric shocks were delivered at a strength twice threshold for perception at  $3 \text{ s}^{-1}$  to the digital nerves of the index finger for FDI, the little finger for ADM, middle finger for MFEDC and the ring finger for RFFDS. Records show the averaged rectified surface EMG signal recorded from the skin overlying the mid-belly of the muscle under study time-locked to each stimulus. In each muscle the longer-latency E2 component is smaller during the power grip. Vertical calibration bar: 20% modulation of mean EMG level. 512 sweeps each record.

The amplitude of the I1 component was found to be significantly smaller during hand support, tripod and power grips compared with that obtained during abduction. However this was not true during any other movement.

The E2 component was much larger during manoeuvres (1)–(4) than during manoeuvres (5)–(8). During finger spreading, index support and hand support the E2 component did not differ significantly in amplitude from that recorded during index abduction. During tripod, power and ball grips and during writing, however, the E2 component was significantly smaller than when elicited during abduction.

Expressing the mean peak amplitudes of the E2 and E1 components as a ratio (E2/E1) this was  $> 1$  when recorded during manoeuvres (1)–(4) and  $< 1$  for manoeuvres (5)–(8).

These experiments revealed that the CMR response recorded from FDI during a relatively independent muscle contraction, such as index finger abduction, differed

from that elicited during one of the grips used in this study. In a second series of experiments, we investigated whether this task dependence could also be seen in other muscles involved in the control of finger movement when the muscle under investigation acted in relative isolation or co-operated with other muscles to produce a grip.

TABLE 2. Mean peak amplitudes and mean integral values for E1 and E2 components of the CMR response recorded in four muscles of the upper limb in five subjects during a relatively isolated movement of the finger and during a power grip.  $n$  = number of subjects  $\times$  trials; theoretical maximum 15. Mean peak amplitude is expressed as percentage modulation of the mean EMG level (s.d.). Integrals are normalized to mean EMG level. LF = little finger, MF = middle finger, RF = ring finger. Isolated finger manoeuvres and power grip have been compared within subjects for each muscle using the  $t$  test for paired data, \* $P < 0.001$ , † $P < 0.01$ , ‡ $P < 0.05$

Muscle manoeuvre	$n$	E1 peak	E2 peak	E2/1 peak	E1 area	E2 area	E2/1 area
<b>FDI</b>							
Abduct index	15	10.6 (1.9)	22.4 (5.6)*	2.1	4.1 (1.5)	9.2 (2.9)*	2.2
Power grip	14	13.4 (4.5)	10.7 (6.2)	0.8	5.4 (2.1)	4.3 (3.4)	0.8
<b>ADM</b>							
Abduct LF	15	11.8 (5.3)	36.6 (24.8)*	3.1	3.8 (2.2)‡	19.7 (18.1)†	5.2
Power grip	13	12.2 (6.3)	10.5 (8.4)	0.9	6.6 (5.3)	4.6 (3.8)	0.7
<b>MFEDC</b>							
Extend MF	15	4.5 (6.6)†	28.0 (12.8)*	6.2	1.4 (2.3)†	11.9 (8.1)*	8.5
Power grip	10	16.1 (8.4)	5.5 (5.9)	0.3	6.2 (3.1)	2.1 (3.1)	0.3
<b>RFFDS</b>							
Flex RF	9	14.0 (16.3)	22.3 (9.5)†	1.6	5.5 (7.2)	8.7 (4.6)‡	1.6
Power grip	8	10.3 (6.8)	8.4 (6.0)	0.8	4.2 (3.4)	2.4 (1.9)	0.6

*Task-dependent changes in the cutaneomuscular reflexes of other muscles of the upper limb involved in the control of finger movement*

Figure 3 shows the change in the CMR responses of four muscles (FDI, ADM, MFEDC, RFFDS) when each was used to produce a relatively independent muscle contraction or a power grip. In each case the longer-latency E2 component was reduced during the power grip.

Table 2 shows the pooled data obtained from five subjects. The amplitude of the E1 component remained relatively constant for the different tasks except in the case of MFEDC where the E1 component was significantly increased during the power grip. In contrast the E2 component showed a consistent and significant reduction during the power grip for every muscle studied.

Expressing the mean peak amplitudes as a ratio of E2 over E1, gave a value  $> 1$  when recorded during a relatively independent muscle contraction and  $< 1$  when recorded during the power grip.

When the reflex electromyograms were analysed by measuring the areas enclosed by the E1 and E2 components rather than by measuring peak amplitudes, very similar results were obtained (Table 2, right-hand three columns) except that the

increase in area of the E1 component during power grip when compared with the relatively isolated finger movement for ADM just reached significance.

### *Needle EMG recording*

These results have been confirmed in two subjects using averaged rectified multi-unit needle EMG recording from FDI, ADM and MFEDC. Representative results are

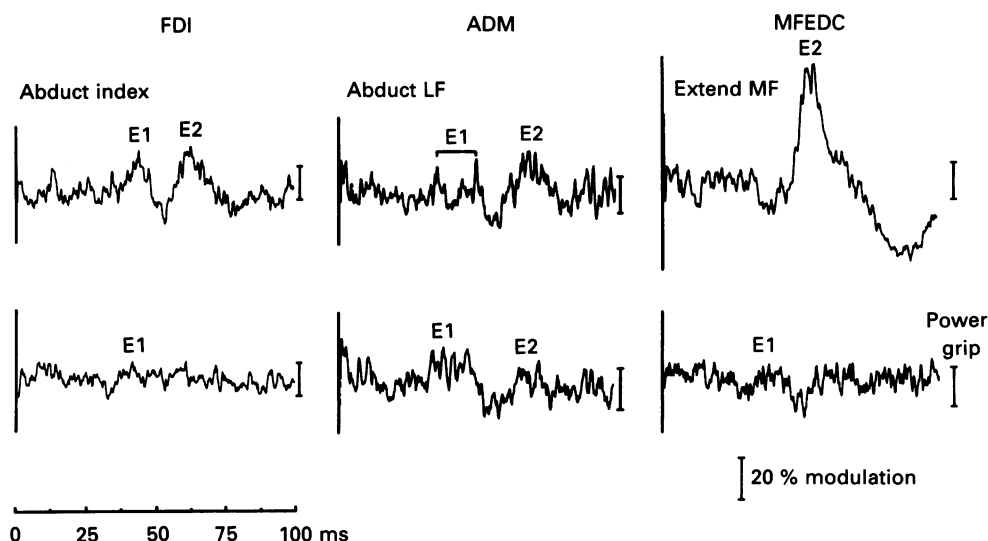


Fig. 4. Cutaneomuscular reflex responses recorded using monopolar concentric needle EMG electrodes from first dorsal interosseous (FDI), abductor digiti minimi (ADM) and the middle finger extensor digitorum communis (MFEDC). Recordings made while the subject performed either a relatively isolated finger movement (top row) or a power grip (bottom row). The relatively isolated contractions were abduction of the index finger, abduction of the little finger and extension of the middle finger. In each case the subject was required to maintain a force of contraction such that the electrical activity recorded from each muscle remained the same at 10–20% of that associated with a maximum voluntary effort. At the same time single electric shocks were delivered at a strength twice threshold for perception at  $3\text{ s}^{-1}$  to the digital nerves of the index finger for FDI, the little finger for ADM, and the middle finger for MFEDC. Records show averaged rectified multi-unit needle EMG signals time-locked to each stimulus. In each muscle the longer-latency E2 component of the cutaneomuscular reflex is smaller during the power grip than when the muscle is used in relative isolation. Vertical calibration bar: 20% modulation of mean EMG level. 512 sweeps each record.

shown in Fig. 4. The data are summarized in Table 3 which shows that the amplitude of the E2 component of the cutaneous reflex of each muscle was larger when the relevant finger was used in a relatively isolated manner than when the same finger participated in a power grip.

### *Fatigue*

Subjects reported that grips were more difficult to maintain than an isolated finger movement. Thus, fatigue has to be considered in relation to the task-dependent effects seen in the CMR. In the first series of experiments, the order of performance of the different tasks was varied. In addition, the first 128 and last 128 sweeps of a



512 sweep recording were compared in seven subjects showing a marked difference in the E2 component between abduction and ball grip. The mean EMG level was the same and the averaged rectified EMG traces were similar in appearance at the beginning and end of the recording for that particular movement. Therefore, fatigue was not associated with the task-dependent change in the CMR.

TABLE 3. Multi-unit needle recordings of the cutaneomuscular reflex response whilst the finger was used in relative isolation and whilst participating in a grip from three muscles of the human upper limb. *n* signifies the number of experiments performed in each subject for each muscle and movement combination. Mean peak amplitudes expressed as % mean EMG level (s.d.)

		Abduct peak			Ball grip peak		
	<i>n</i>	E1	E2	<i>n</i>	E1	E2	
FDI							
Subject 1	2	17.5 (1.1)	37.0 (0.8)	2	15.9 (1.2)	14.5 (0.8)	
Subject 2	3	18.7 (3.5)	22.7 (5.8)	3	21.1 (5.8)	11.2 (2.8)	
		Abduct peak			Power grip peak		
FDI							
Subject 1	3	10.7 (1.7)	38.9 (9.8)	3	17.3 (1.1)	30.2 (8.2)	
ADM							
Subject 1	10	13.0 (5.7)	23.0 (6.8)	7	10.7 (8.1)	16.5 (7.4)	
Subject 2	3	8.7 (7.8)	22.1 (3.0)	3	17.5 (0.9)	14.6 (8.4)	
MFEDC							
Subject 1	3	0	40.5 (13.3)	2	6.8 (9.6)	10.8 (2.4)	
Subject 2	3	0	55.6 (9.9)	2	2.4 (3.4)	2.4 (3.4)	

#### DISCUSSION

Muscles in the hand and forearm take part in movements that can be broadly classified as those when a finger acts in relative isolation and those in which a number of fingers act together, for example, the power grip (Napier, 1956). It is clear from the present results that cutaneomuscular reflexes elicited during performance of the former are very different from those elicited during the latter. The long-latency second excitatory component (E2) of the reflex is the predominant component elicited when the subject carries out a manoeuvre in which a finger acts in relative isolation. It decreases significantly when elicited from the same muscle participating in the grips studied in these experiments. The same result was found for all muscles studied whether they were intrinsic hand muscles (FDI, ADM) or forearm finger flexor or extensor muscles (RFFDS, MFEDC).

There are a number of possible explanations for this result, which will be considered in turn.

#### *Changes in afferent input*

The size of the sensory nerve volley recorded over the median nerve at the wrist elicited by digital nerve stimulation remained the same during a relatively isolated finger manoeuvre and during grips. This result indicates that the size of the afferent volley set up by the electrical stimulus was not affected by changing the position of the hand and fingers for the different manoeuvres. Background afferent activity.

however, inevitably changes with each task. An attempt was made to minimize this factor by the subjects making the independent finger movements of index finger abduction and spreading of the fingers with the hand held flat on the table top. In this way the area of skin in contact with a surface was similar to that during a grip. We do not, however, believe this is an important consideration, as during index support the area of skin contact was just one finger tip and during hand support it was all the finger tips, yet the CMR response had a similar configuration to that found during index abduction when the whole of the palm of the hand was in contact with a surface. Differences in background cutaneous afferent input do not appear to be related to the task-dependent changes in cutaneous reflexes observed in the present study.

Background joint receptor and muscle afferent input must also differ when the different tasks are performed. For grips, the hand positions adopted involved predominantly finger flexion which would tend to increase joint receptor input. However, the CMR responses recorded during index abduction whilst the remaining fingers were flexed rather than extended also showed a dominant E2 component. The input from muscle afferents will depend on the number of muscles that are active. Nevertheless, a task-dependent difference was found between cutaneous reflexes recorded during finger spreading and grip when a comparable number of muscles was involved.

#### *Changes in central excitability*

Evidence from an earlier study suggested that the short-latency excitatory and inhibitory components (E1, I1) of the cutanocomuscular reflex response are mediated along spinal pathways and that the following longer-latency excitatory component (E2) is of supraspinal origin requiring the integrity of the dorsal columns, sensorimotor cortex and corticospinal tract (Jenner & Stephens, 1982). The results of the present experiments suggest that the latter pathways are more active in response to cutaneous inputs when a finger acts in relative isolation than when several fingers co-operate to produce grips such as those used in this study.

Central gating of sensory information has been extensively demonstrated. At the level of the dorsal column nuclei, for example, voluntary movement by the cat will lead to a reduction in the lemniscal response to electrical stimulation of the radial nerve (Ghez & Pisa, 1972; Coulter, 1974). Recordings from cells of the motor cortex have revealed that the discharge pattern in response to electrical cutaneous stimulation is dependent on the phase of the step cycle (Palmer, Marks & Bak, 1985). Evarts & Fromm (1977) concluded from their study of motor cortical cells that the discharge of these neurones is continuously modulated by sensory feedback, particularly when accurate positioning and fine movement is required. During large ballistic movements of the wrist, modulation was much reduced. It is therefore possible that the afferent volley produced during those grips employed in the present study is subjected to a greater degree of gating than that occurring during a more isolated voluntary contraction, with the result that the cutaneous input to the cortex is lower during the grips.

The level of excitability of the motor cortex has been shown to be dependent on the motor task. Such changes could account for the task-dependent changes in the CMR that we have observed. In the monkey, some of the pyramidal tract cells in the

motor cortex projecting to finger muscles are more active during a precision grip, which is considered to be a relatively independent finger movement, than during a power grip (Muir & Lemon, 1983; Buys, Lemon, Mantel & Muir, 1986). A previous study showed that almost half of those pyramidal tract cells studied received afferent input from the fingers (Lemon, 1981). Thus these cells could be expected to produce a larger change in output for a given cutaneous afferent input during a relatively isolated finger movement than during a grip and thus produce a larger longer-latency excitatory response E2 in their target muscles. This is considered in more detail in an accompanying paper (Datta, Harrison & Stephens, 1989).

Taking the size of the E2 component as an indication of activity in the supraspinal pathways believed to be involved in the CMR, there appears to be a progressive reduction in activity from the most independent finger movements (such as index finger abduction or middle finger extension), through intermediate manoeuvres where several fingers act together (such as hand support or tripod grip), to whole hand grips where many muscles act together to move all the fingers. During writing, the configuration of the CMR response recorded from FDI was similar to that seen during a grip. Thus it appears that FDI is participating in a grip during writing; the fine finger movements being governed by the forearm muscles.

#### *Task-dependent changes in the spinal components of the cutaneomuscular reflex*

The size of the short latency E1 and I1 components remained essentially unchanged during the different tasks. However, the few changes that were seen occurred during the less independent finger movements or grips and consisted of an increase in E1 amplitude or a decrease in I1 amplitude. In an earlier study it was found that patients with central motor lesions producing signs of corticospinal tract involvement exhibited an increased E1 component and a decreased I1 component (Jenner & Stephens, 1982). In neonates, where the corticospinal tract has yet to reach functional maturity, the CMR consists solely of an E1 component (Issler & Stephens, 1983). Taken together, these observations suggest that the spinal pathways mediating the E1 component are made less active and those mediating the I1 component made more active by corticospinal activity associated with relatively isolated finger movements.

The marked task-dependent changes in reflex activity observed in the present study serve to reinforce the importance of defining carefully the behavioural context when studying cutaneous reflexes in muscles controlling finger movement. This may also be true for the study of other reflexes such as those elicited by muscle stretch. Certainly the design of experiments must now take these factors into account. Indeed, in this way previously unexpected and unexplored mechanisms by which reflex motor behaviour in man is adapted to its functional context may be revealed.

This work was supported by grant number A/8/1392 from Action Research for the Crippled Child.

#### REFERENCES

- BUYS, E. J., LEMON, R. N., MANTEL, G. W. H. & MUIR, R. B. (1986). Selective facilitation of different hand muscles by single corticospinal neurones in the conscious monkey. *Journal of Physiology* **381**, 529–549.

- CACCIA, M. R., MCCOMAS, A. J., UPTON, A. R. M. & BLOGG, T. (1973). Cutaneous reflexes in small muscles of the hand. *Journal of Neurology, Neurosurgery and Psychiatry* **36**, 960-977.
- COULTER, J. D. (1974). Sensory transmission through lemniscal pathway during voluntary movement in the cat. *Journal of Neurophysiology* **37**, 831-845.
- DATTA, A. K., HARRISON, L. M. & STEPHENS, J. A. (1989). Task-dependent changes in the size of the motor response to magnetic brain stimulation studied in human first dorsal interosseous muscle. *Journal of Physiology* **418**, 13-23.
- EVANS, A. L., HARRISON, L. M. & STEPHENS, J. A. (1986). Task-dependent changes in the cutaneomuscular reflex response in human first dorsal interosseous muscle. *Journal of Physiology* **381**, 47P.
- EVANS, A. L., HARRISON, L. M. & STEPHENS, J. A. (1987). Task-dependent changes in the cutaneomuscular reflex response in various muscles of the human upper limb. *Journal of Physiology* **398**, 43P.
- EVARTS, E. V. & FROMM, C. (1977). Sensory responses in motor cortex neurones during precise motor control. *Neuroscience Letters* **5**, 267-272.
- FORSSBERG, H., GRILLNER, S. & ROSSIGNOL, S. (1975). Phase dependent reflex reversal during walking in chronic spinal cats. *Brain Research* **85**, 103-107.
- FORSSBERG, H., GRILLNER, S. & ROSSIGNOL, S. (1977). Phasic gain control of reflexes from the dorsum of the paw during spinal locomotion. *Brain Research* **132**, 121-139.
- GHEZ, C. & PISA, M. (1972). Inhibition of afferent transmission in cuneate nucleus during voluntary movement in the cat. *Brain Research* **40**, 145-151.
- ISSLER, H. & STEPHENS, J. A. (1983). The maturation of cutaneous reflexes studied in the upper limb in man. *Journal of Physiology* **335**, 643-654.
- JENNER, J. R. & STEPHENS, J. A. (1982). Cutaneous reflex responses and their central nervous pathways studied in man. *Journal of Physiology* **333**, 405-419.
- KANDA, K. & SATO, H. (1983). Reflex responses of human thigh muscles to non-noxious sural stimulation during stepping. *Brain Research* **288**, 378-380.
- LEMON, R. N. (1981). Functional properties of monkey motor cortex neurones receiving afferent input from the hand and fingers. *Journal of Physiology* **311**, 497-519.
- MUIR, R. B. & LEMON, R. N. (1983). Corticospinal neurones with a role in precision grip. *Brain Research* **261**, 312-316.
- NAPIER, J. R. (1956). The prehensile movements of the human hand. *Journal of Bone and Joint Surgery* **38B**, 902-913.
- PALMER, C. I., MARKS, W. B. & BAK, M. J. (1985). The responses of cat motor cortical units to electrical cutaneous stimulation during locomotion and during lifting, falling and landing. *Experimental Brain Research* **58**, 102-116.
- PROCHAZKA, A., SONTAG, K. H. & WAND, P. (1978). Motor reactions to perturbations of gait: proprioceptive and somesthetic involvement. *Neuroscience Letters* **7**, 35-39.
- ROSENBLUM, L. & HORTON, M. E. (1971). The maturation of fine prehension in young children. *Developmental Medicine and Child Neurology* **13**, 3-8.
- WYNN-PARRY, C. B. (1966). *Rehabilitation of the Hand*, 2nd edn, London: Butterworth.